Activity patterns in northern rock sole are mediated by temperature and feeding history

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Abstract

Studies of activity patterns of fishes rarely consider the impact of environmental conditions or organism state. In this paper we demonstrate the influence of temperature and feeding history on the diel activity patterns of juvenile (age 1+) northern rock sole *Lepidopsetta polyxystra* (Orr and Matarese). Activity type (benthic vs. water column) and level were determined from hourly video recordings of fish in laboratory tanks with the aid of infrared illumination. Groups of rock sole ($n = 4$ per group) were observed at 2, 5, 9 and 13 °C without food and at 9 °C with food offered once in the morning, at dusk or at night. In all experiments, rock sole exhibited peak activity levels during the dusk and dawn transition periods and a temporal segregation of activity mode. Daytime and crepuscular activity was predominantly benthic, occurring within a few centimeters of the tank bottom, whereas a significant fraction of nighttime activity (up to 90%) occurred with rock sole swimming in the water column or at the water surface. The primary effect of water temperature on rock sole behavior was a reduction in daytime and crepuscular activity at low temperatures. Conversely, nighttime activity levels were independent of water temperature, resulting in a thermally induced shift in the primary activity period. Morning and dusk feeding produced a short-term (1 h) elevation in activity followed by activity suppression until the subsequent crepuscular phase. Nighttime feeding resulted in a longer period of elevated activity (2 h) and did not suppress further benthic or water column activity. These observations suggest a temporal segregation of activity between daytime foraging and nighttime movement that balances energetic demands with predation risk. Published by Elsevier B.V.

Keywords: Activity; Behavior; Diel cycle; Flatfish; *Lepidopsetta polyxystra*

1. Introduction

Organisms are commonly classified as diurnal, nocturnal or crepuscular based on their predominant activity phase. Alternatively, activity may be scheduled to coincide with other regular changes in the environment such as tidal fluctuations. Laboratory

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and field investigations have demonstrated considerable plasticity in the diel activity rhythms of various fishes (see review by Reebs, 2003). In many cases, laboratory-cultured fish adjust activity schedules to regular feeding intervals, referred to as "feeding anticipatory activity" (Sánchez-Vázquez and Madrid, 2001). Natural phenomena include a switch to daytime activity in high-latitude burbot *Lota lota* (Müller, 1978) and a switch to nocturnalism among overwintering minnows (Fraser et al., 1993). An organism's expressed activity pattern depends on the interaction of proximate factors that alter behavior (prey availability, predator presence) and an endogenous rhythm that itself may vary with environmental conditions and ontogenetic stage (Noakes, 1992).

While the basic behavior patterns of some flatfishes have been described, the influence of habitat characteristics and fish condition have rarely been explored. For example, variation in trawl catch rates may be evidence of temperature's influence on the behavior of adult sole (Horwood and Millner, 1998), but the nature of this effect is unknown. The most extensive investigations of juvenile flatfish activity patterns have been made for plaice *Pleuronectes platessa*(L.) and sole *Solea solea* (L.). After recruiting to shallow nursery grounds, plaice make tidal migrations to forage on intertidal mud flats (Gibson, 1973). However, this tidally synchronized activity is additionally affected by the day–night cycle (Burrows et al., 1994) and presence of prey and predators (Burrows and Gibson, 1995). For flatfish residing in less tidally influenced habitats, a diel rhythm appears to dominate activity (Gibson et al., 1998).

Flatfishes exhibit dramatic morphological and behavioral adaptations to a benthic lifestyle. While most activity occurs on or near the benthos, flatfishes are not restricted to the benthic environment. Several large piscivores such as Pacific halibut *Hippoglossus stenolepis* (Schmidt) make extended foraging excursions in the water column. However, for most flatfish species, extended periods of water column activity appear restricted to nighttime. Adult sole and plaice may use nighttime swimming in conjunction with tidal stream transport in spawning migrations (de Veen, 1967; Arnold and Metcalfe, 1995). Juveniles of several species also exhibit some level of nighttime activity in the water column (Champalbert and Castlebon, 1989; Burrows, 1994), but the role of this behavior in fishes with such tight associations to the bottom is poorly understood.

In this paper, we describe the behavioral patterns of juvenile northern rock sole *Lepidopsetta polyxystra* (Orr and Matarese) based on laboratory observations. In particular we examine the diel activity pattern across the range of temperatures likely encountered in shallow waters of the northern Gulf of Alaska. The general effects of foraging success on activity rhythm are described by feeding at different times during the daily cycle. We also determine the range of conditions under which rock sole exhibit nighttime water column swimming.

2. Materials and methods

2.1. Study organism

Northern rock sole are an important component of North Pacific fisheries and foodwebs, ranging from the Bering Sea to Puget Sound, USA. In the Gulf of Alaska, spawning occurs in winter and juveniles recruit to shallow subtidal (<50 m depth) habitats in early summer (Norcross et al., 1997; Abookire and Norcross, 1998). Juvenile rock sole are effective background mimics and use burial and crypsis as primary anti-predator tactics (Ryer et al., 2004). In addition to the seasonal temperature cycle, there is significant spatial variation in bottom water temperatures throughout the species range. Behavioral observations of rock sole are limited to habitat choice (Stoner and Ottmar, 2003; Stoner and Titgen, 2003), predation vulnerability (Ryer et al., 2004) and a tendency to aggregate in laboratory tanks (Moles and Scott, 2002). Field data from the Bering Sea indicates that rock sole feed diurnally with a possible peak in feeding intensity near dawn (Corcobado Oñate, 1991; Lang, 1992). Circadian activity patterns have not been described for northern rock sole or any co-occurring North Pacific flatfish.

2.2. Capture and holding

Juvenile (age-0) northern rock sole, 20–40 mm total length (TL), were captured from nearshore (7–20 m depth) nursery grounds in the vicinity of Kodiak Island, Alaska, in July 2002. After several

days' holding at the Alaska Fisheries Science Center's (AFSC) Kodiak laboratory, fish were shipped overnight in insulated containers to the AFSC's Newport, Oregon, laboratory. Fish were reared initially in $64 \times 45 \times 23$ cm tanks at densities of 20 fish/tank. Each day, rock sole were fed a combination of thawed *Artemia* sp. and commercially available fish food (1 mm pellets initially, 2 mm pellets later). The time of feeding varied but always occurred during the daily light phase. In late October, fish were transferred to 183 cm diameter round tanks and feeding was reduced to 3 times per week. Temperature during the holding period was 9 ± 1.5 °C, except for acclimation prior to Temperature Trials. Photoperiod during holding prior to Temperature Trials was 17:7 light/dark and changed to 12:12 prior to Feeding Trials to increase sampling coverage of the dark and transitional periods. Individual fish were used only once within each set of trials, but may have been used in both Temperature and Feeding Trials, conducted 3 months apart.

2.3. Experimental observations

Observations were made in duplicate 1.9 m diameter × 0.75 m depth tanks equipped with remotely monitored overhead cameras. Both experimental tanks had three independent light sources: a ring of six 60-W incandescent bulbs in reflecting cones 1.8 m above the water surface provided daytime illumination ($\sim 3.3 \cdot 10^{-1}$ μmol photons m^{-2} s^{-1} at the water surface); a ring of 10 green LED clusters 1.5 m above the water surface provided dim light used to transition between day and night ($\sim 1.1 \cdot 10^{-3}$ μmol photons m^{-2} s^{-1}); and four 60-W LED infrared illuminators beneath the tank allowed observations to be made in darkness ($< 4.0 \cdot 10^{-7}$ μmol photons m^{-2} s^{-1}). The infrared light used to illuminate the tank is beyond the spectral sensitivity of fishes as peak wavelength from the infrared emitters was 880 nm, with no emissions below 760 nm. A camera with sensitivity to infrared light was mounted 2.4 m above the water surface and connected to a video recorder in another room. Experimental light intensities matched those observed in age-0 rock sole habitats. The transition between darkness and dim light occurred gradually over a period of 15 min and was completed 30 min prior to subsequent observations.

The transition between dim and daylight was instantaneous and occurred 45 min prior to subsequent observations. For Temperature Trials (with smaller fish), a transparent inner wall was used to reduce the tank diameter to 105 cm, and cameras zoomed in to ensure visualization of the fish. A thin layer of sand covered the tank bottom. Additional details on the design of the experimental tank (including diagram) can be found in Ryer and Olla (1998).

Preliminary observations on the activity patterns of rock sole were used to verify observation methods and develop activity metrics. With only a thin layer of sand covering the tank bottom (to allow IR passage), the fish were unable to cover themselves completely with sediment, but characteristic burial behavior was frequently observed. Daytime observations of fish in the observation tanks with deep (~ 5 cm) and thin layers of sand did not indicate any significant differences in overall activity levels. Sequential observation of tank regions confirmed that all lateral movements of rock sole were observed during complete tank observations.

2.4. Temperature Trials

Three months prior to Temperature Trials, 150 rock sole were randomly assigned to the temperature treatments of 2, 5, 9, and 13 °C (Table 1). After transferring the fish, temperatures in the acclimation tanks ($64 \times 45 \times 23$ cm) were raised or lowered to the test temperature by 1 °C day^{-1}. For each trial, 4 rock sole were captured from acclimation tanks, measured (to 1

Table 1
Summary of experimental conditions examining the diel periodicity of activity in juvenile northern rock sole

Treatment	n	Mean TL	Range	Start time	Photoperiod cycle (h)			
					Day	Dusk	Night	Dawn
Temperature trials (February–March 2003)								
2°	5	70.6	59–88	1500	15	1	7	1
5°	5	71.9	57–82	1500	15	1	7	1
9°	5	74.6	57–104	1500	15	1	7	1
13°	5	77.0	52–101	1500	15	1	7	1
Feeding trials (May–July 2003)								
0900	9	94.5	85–114	900	6	3	12	3
1700	3	88.8	80–97	900	6	3	12	3
2100	4	102.3	94–119	900	6	3	12	3

mm TL) and introduced into the experimental tank. Fish were acclimated to the experimental tank for 1 day during which food was not available. Beginning at 1500 on the following day (~23-h post-introduction; 48-h post-feeding), fish activity was monitored by video recordings of the entire tank during the final 15 min of each hour. After 24 h, the fish were removed from the observation tanks and new groups introduced for acclimation. Fish were not fed while in the observation tanks. Photoperiod in the observation tanks differed from acclimation tanks in that a 1-h period of dim light was used as a transition between the daylight and dark periods while maintaining the nighttime duration of 7 h.

2.5. Feeding Trials

Feeding Trials were designed to examine the direct effect of feeding on activity levels of rock sole rather than entrainment of activity patterns to a specific feeding regime. Rock sole were introduced into the observation tanks in groups of four. Beginning at 0900 on the second day of acclimation, video-recordings were made of the final 15 min of each hour for the next 24 h. Fish were fed once during the tank acclimation period and once during the 24-h observation period. Feeding during the experimental observation period occurred at 0900, 1700 or 2100, with treatments referred to, respectively, as daytime, evening and night feeding. The feeding during the tank acclimation period was adjusted such that it fell 48–56 h prior to the feeding during the observation period. The photoperiod of 12-h full light and 12-h dark during holding was altered such that 3 h at the beginning and end of the daylight period had dim rather than full light. The 12-h period of darkness was unchanged from acclimation.

2.6. Analysis

Behavioral observations of juvenile rock sole were based on analysis of 5–10 min of the video recordings made during each hour of both experiments. Behavioral observations were made separately for each fish in the group at each observation interval, but fish could not be identified across intervals (hour-to-hour). A grid dividing the tank into six radial sections

was overlaid on the video monitor during playback and the number of line crossings was used as an index of distance traveled. A fish was considered active from its first movement until its last movement prior to remaining stationary for longer than 30 s or exhibiting burial behavior.

Most activity consisted of short (<3 body length), saltatory movements along the sediment surface, interspersed with motionless periods of varying duration. Less frequently, fish were observed swimming in the water column. In some cases, rock sole were observed swimming along the tank wall off the substrate which appears to be an artifact of tank confinement. This swimming activity along the wall was much more common in the Temperature Trials when a transparent wall was used to confine fish to a reduced tank area, and the fish frequently moved back and forth along the same section as though attempting to navigate an obstacle. Therefore, this activity was included in measures of active time, but line crossings made while swimming in contact with the tank wall were not included in the analysis. Subsequent references to "swimming" refer exclusively to activity in the water column, away from the wall and preceded by direct movement from the sediment surface to the water surface (note this usage of "swimming" differs from those of Gibson, 1980; Kellison et al., 2000 and is analogous to the "rise" behavior in Burrows, 1994).

During each observation period two measures of activity were recorded for each of the 4 fish in the group: the total active time (s min^{-1}) and the frequency of line crossings (per 5 min). The group mean activity score for each hour was used as the level of measurement in analyses. Line crossings were categorized as benthic (in contact with substrate) or water column (off bottom but not in contact with tank wall). We also noted any interactions between fish, categorized as avoidance (a stationary fish moved away from an approaching fish), aggressive (only 1 observation of overt aggression) or coordinated (2 fish moving roughly parallel in an alternating pattern).

For statistical analysis of diel activity patterns, observations for each group of fish were averaged for continuous time periods or for specific light levels. Analysis of activity levels (active time and line crossings) across time periods within treatments was based

on repeated measures ANOVA. Single classification ANOVA was used for comparisons of activity in specific time periods across experimental treatments. Specific post-hoc comparisons were made with Fish-er's LSD test. Departures from homoscedasticity were restricted to comparisons involving periods with near zero activity levels and therefore did not significantly impact statistical analyses. *G*-tests of independence of
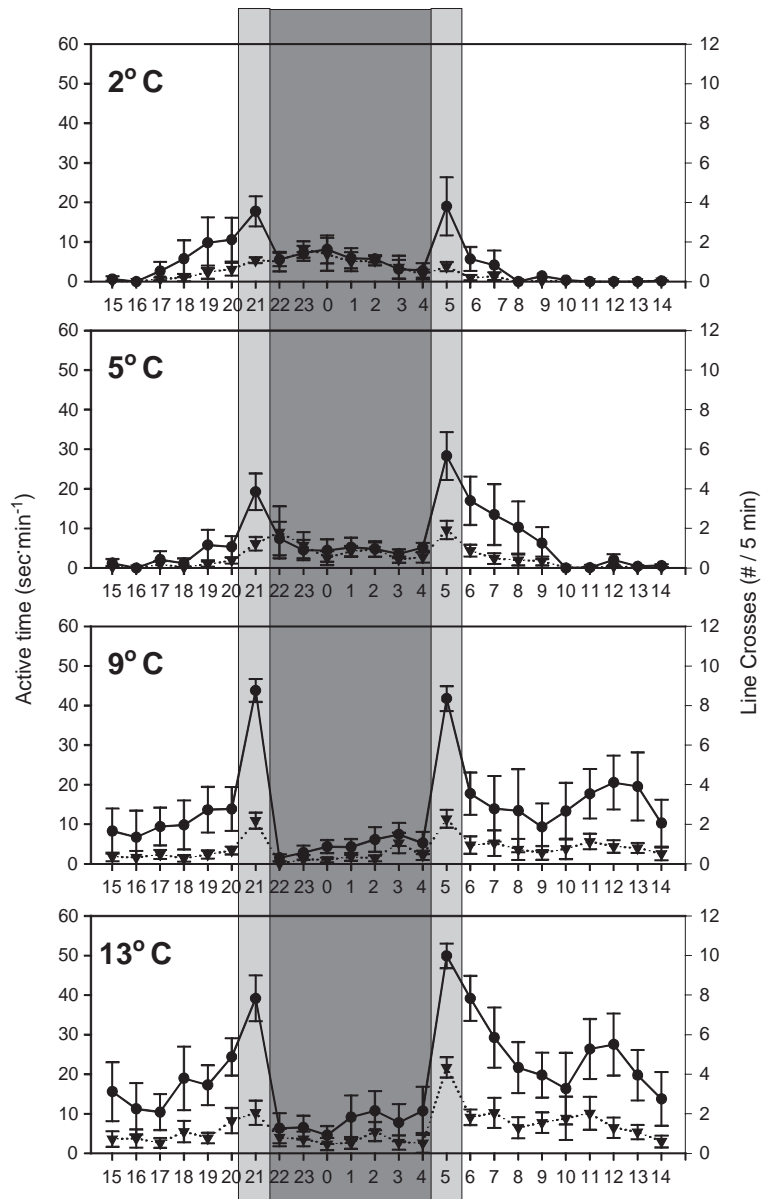

Fig. 1. Diel activity patterns of juvenile northern rock sole at 2–13 °C. Crepuscular and nighttime periods are indicated by light and dark boxes, respectively. Circles represent mean active time, triangles represent mean number of line crossings. Error bars indicate 1 S.E. of mean of 5 replicates at each temperature.

line crossing counts were used to determine relationships between activity type (benthic vs. water column) and environmental conditions (light level, temperature and feeding history).

3. Results

3.1. Temperature Trials

Northern rock sole displayed a marked crepuscular periodicity in activity with daytime, dawn and dusk activity levels significantly affected by temperature (Repeated measures ANOVA, $df = 6,32$, $P = 0.01$; Fig. 1). Active time was significantly higher in the low light levels of dusk and dawn than during day or night at all temperatures (Post-hoc LSD comparisons, $P < 0.05$). The frequency of line crossings was significantly higher during crepuscular periods than during day and night only in the 9 and 13° treatments ($P < 0.05$). The level of crepuscular activity (dusk and dawn averaged) was strongly temperature dependent ($df = 3,16$, $P < 0.001$), increasing from 18 s min^{-1} at 2° to 43 s min^{-1} at 9 and 13°.

Daytime activity was less than that of dusk and dawn, but displayed a similar pattern of temperature-dependence. Active times averaged less than 3 s min^{-1} at 2° and 5°, increasing to 32 s min^{-1} at 13°. Counts of line crossings had a similar pattern of temperature dependence. Unlike other periods, nighttime activity levels were uniformly low and not significantly affected by temperature ($df = 3,1$, $P = 0.851$), averaging only 5 s min^{-1} across all treatments.

The small amount of nighttime activity observed frequently included sustained off-bottom swimming. 89.9% of nighttime line crossings occurring while swimming off bottom (Fig. 2). The fraction of night-time line crossings that were made in the water column was significantly affected by temperature (G-test of independence, $G_{adj} = 27.01$, $P < 0.001$), increasing as water temperature decreased. Activity during the daytime and crepuscular periods occurred almost exclusively in contact with the sediment surface. Only 3.4% and 15.4% of daytime and crepuscular line crossings occurred in the water column. This fraction was independent of water temperature for daytime ($G_{adj} = 3.55$, $P = 0.314$). The interaction
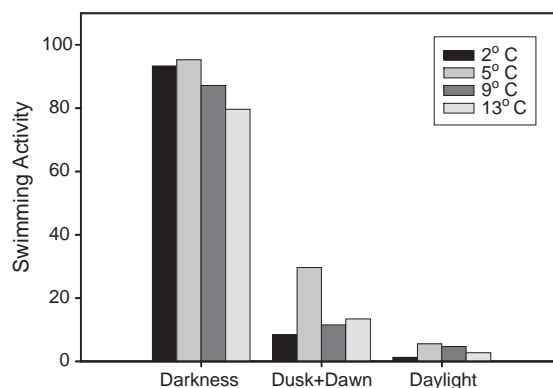

Fig. 2. Water column swimming of juvenile rock sole as a function of light level and water temperature. Bars represent the fraction of all line crossings at each light level made while swimming in the water column.

between temperature and swimming activity ($G_{adj} = 12.52$, $P = 0.006$) observed during the crepuscular periods was due to an unusually high number of swimming crosses observed in one 5° replicate (15 of 21 observations). There was no effect of temperature on crepuscular activity mode with this replicate removed ($G_{adj} = 0.92$, $P = 0.826$).

3.2. Feeding Trials

A strong crepuscular pattern of rock sole activity was observed in the Feeding Trials (Repeated measures ANOVA, $df = 6,39$; Fig. 3). Active time and line crossings were significantly higher during the dawn and dusk periods than during the day and night in all treatments (Post-hoc comparisons $P < 0.05$) with the exception that dawn activity in the evening feeding treatment was not significantly higher than day and night activity levels ($P > 0.05$).

Feeding influenced the activity of northern rock sole, but not the overall crepuscular periodicity of activity. In all trials, the introduction of food resulted in a marked increase in activity levels. We could not determine if this activity represented continued feeding as food particles were too small to see on video and rock sole did not exhibit stereotypical feeding behaviors distinguishable from routine activity. This brief period of activity following feeding was followed by extended periods of inactivity in two of the three treatments. When feeding occurred in the morning, fish were inactive for the remainder of the
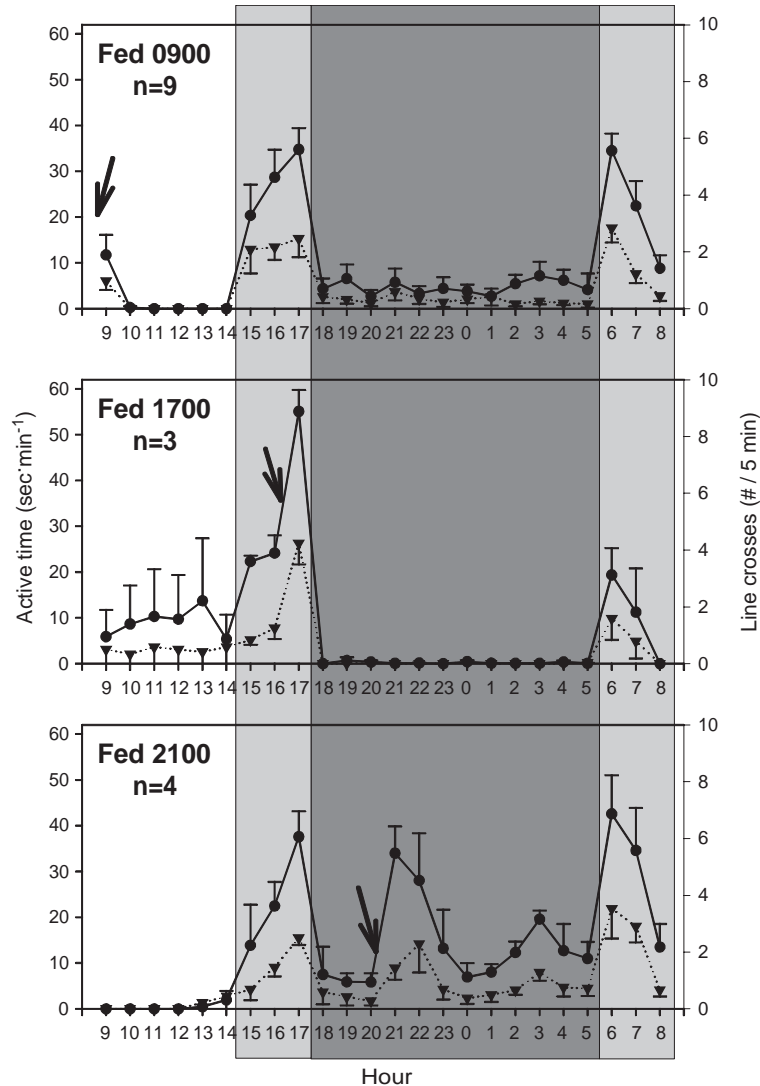
Fig. 3. Effect of feeding on diel activity pattern in rock sole. Arrows indicate the time of feeding. Circles represent mean active time, triangles represent mean number of line crossings. Error bars indicate 1 S.E. of mean of replicates.

day, resuming activity at dusk. When feeding occurred in evening, fish remained inactive for the duration of the nighttime, resuming activity at dawn. Conversely, the cessation of activity was not observed following night feeding.

Of the four time periods examined (day, dusk, night and dawn), only nighttime activity levels differed significantly among the feeding treatments (ANOVA, $df=2,13$, $P=0.004$). Nighttime activity was highest (averaging 14 s min^{-1}) following feeding

at night, intermediate following a morning feeding (5 s min^{-1}), and strongly suppressed by feeding in the evening (only 0.2 s min^{-1}).

Water column swimming of rock sole was frequently observed at night, while activity during lit periods was almost exclusively benthic (Fig. 4). Fewer than 2% of all line crossings observed under daylight or the dim light of dawn and dusk were made by fish swimming in the water column. Conversely, 52% of line crossings observed at night were made by
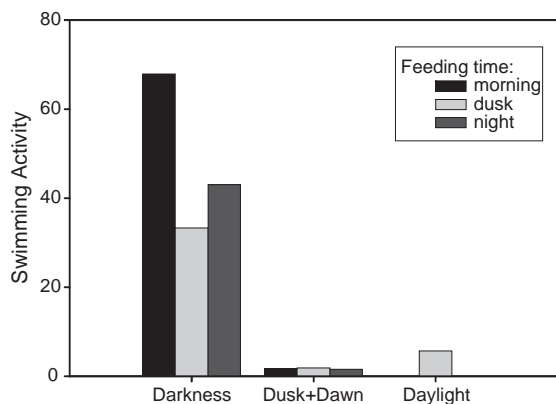
Fig. 4. Water column swimming of juvenile rock sole as a function of light level and feeding time. Bars represent the fraction of all line crossings at each light level made while swimming in the water column.

fish swimming in the water column away from tank walls.

4. Discussion

4.1. Crepuscular pattern

Infrared light-assisted laboratory observations of juvenile northern rock sole demonstrated a distinct crepuscular activity pattern. While water temperature and feeding history significantly affected the activity levels of rock sole these factors did not alter the overall pattern of dusk and dawn activity peaks. This is an important observation as laboratory experiments have generally characterized flatfishes as diurnal or nocturnal. However, most previous laboratory studies of activity patterns in flatfishes used a light–dark cycle that did not include transitional periods. A strong crepuscular periodicity of activity was also observed in an in situ study of the movements of juvenile plaice (Gibson et al., 1998).

These experiments likely capture the dominant cycles of rock sole activity, whether they are primarily driven by entrained rhythms or by direct responses to light as the experimental levels are consistent with those experienced by juvenile rock sole in the wild. Surface light levels and extinction coefficients were measured at the collection site during a period of moderate turbidity in August 2004. Midday light

levels estimated at 15 m depth, the center of observed rock sole distribution at this site, averaged 1.04 μmol photons m^{-2} s^{-1}, similar to or greater than daytime levels used in the laboratory experiment (0.33 μmol photons m^{-2} s^{-1}). Nighttime light levels (with overcast sky) were below $1.0 \cdot 10^{-6}$ μmol photons m^{-2} s^{-1} (3 orders of magnitude below experimental dusk/dawn levels).

Both an entrained rhythm and a direct response to light level appear to contribute the crepuscular activity pattern of northern rock sole. This is evident in the Temperature Trials where activity levels began increasing several hours prior to the dusk transition and declined to mid-day minimums over a similar period following the dawn transition. However, the peak activity levels observed during the dawn and dusk transition periods were substantially higher than in the adjacent daylight hour, suggesting a direct response to the intermediate light levels of dusk and dawn. Furthermore, as dusk and dawn transitions were not incorporated in the temperature acclimation phase, fish experienced only a single cycle of transitional light levels prior to experimental observations (during tank acclimation) and therefore would not have anticipated their occurrence.

Activity patterns linked to local tidal cycles have been identified in several species of flatfishes (Gibson, 1973; Burrows et al., 1994). The potential for such rhythms in northern rock sole could not be examined in this study because fish had been maintained for an extended period under laboratory conditions. As juvenile northern rock sole reside in subtidal habitats (to 50 m), there is little potential for stranding in unfavorable habitats, a common explanation for tidal activity rhythms (Gibson, 2005). However, activity might be timed to coincide with tidal currents that result in increased abundance or availability of prey.

4.2. Nighttime swimming

Nighttime off-bottom or surface-swimming has been observed in the field and laboratory in a number of flatfish species (Verheijen and de Groot, 1967; Champalbert et al., 1992; Burrows, 1994). As this swimming occurred away from tank walls and was initiated by direct ascent to the water surface, these observations of swimming activity represent a natural

behavior, rather than the effects of tank confinement. Nighttime swimming was a consistent component of rock sole activity in all experimental treatments (except following dusk feeding when all activity was suppressed) accounting for up to 90% of line crossings made at night. The contribution of off-bottom swimming to flatfish activity has rarely been quantified, but Champalbert et al. (1992) found it comprised over 50% of nighttime activity in juvenile sole. As in other species, this swimming was rare during daylight or crepuscular periods. Subsequent experiments with juvenile rock sole suggest that this behavior is commonly observed at light levels of $2.0 \cdot 10^{-5}$ μmol photons m^{-2} s^{-1} and below (Hurst, unpublished observations). The general characteristics of flatfish swimming are described in Gibson (2005). In juvenile rock sole, this behavior was characterized by a lifting of the anterior half of the body from the sediment surface and direct vertical swimming to the water surface. At the surface the fish reoriented and began moving horizontally, alternately swimming and gliding before returning to the substrate.

Presumably, the conspicuousness and limited maneuverability of most flatfishes away from the bottom makes them highly vulnerable to visual predators, restricting flatfish to residence on or near the bottom during the day. This is supported by the increased predation vulnerability of hatchery reared flatfish that appears related to increased levels of daytime off-bottom activity (Furuta, 1996; Kellison et al., 2000). The reduced risk of visual predation at night may allow water column activity. In fact evidence indicates that nighttime swimming activity is an integral component of migratory movements throughout the life history of many flatfishes. Nighttime activity is tightly linked to tidal cycles in promoting the transport of larval fishes to nursery areas (Miller et al., 1991; Burke et al., 1998). In addition, nighttime surface swimming has been observed in association with spawning migrations of sole and plaice (de Veen, 1967; Arnold and Metcalfe, 1995). The widespread nature of this behavior implies that nighttime swimming is energetically more efficient or incurs less predation risk than covering a similar distance by moving along the bottom. While appealing, such theories have not been experimentally examined.

Juvenile flatfish may use nighttime swimming to migrate between or "sample" habitats on smaller scales. The importance of nighttime swimming in the daily tidal migrations of juvenile plaice and dab *Limanda limanda* (L.) was suggested by Burrows et al. (1994). Creutzberg et al. (1978) showed that metamorphosing larval plaice increased water column swimming following starvation and remained on the sediment surface following feeding, promoting retention in suitable foraging habitats. For northern rock sole, the latter explanation may be more applicable as preliminary data from a Kodiak nursery area suggest that juvenile rock sole do not undertake extensive diel or tidal migrations (Hurst, unpublished data).

Anecdotal observations of crab megalopae in the stomachs of Pacific sand dab (*Citharichthys sordidus*, Girard) captured in mid-water trawls at night (R. Emmett, NWFSC Newport OR, personal communication) suggest that nighttime foraging in the water column is possible for at least some flatfish species. However, the nighttime light levels used in these experiments ($<4.0 \cdot 10^{-7}$ μmol photons m^{-2} s^{-1}) are well below the threshold level necessary for visual foraging in most fishes (Hunter, 1968; McMahon and Holanov, 1995; Ryer and Olla, 1999; Stoner, 2003). Clearly, further work is required to understand the function of this behavior in juvenile flatfishes.

4.3. Thermal effects

Despite the regulatory role of temperature in most facets of ectotherm physiology and ecology including swimming performance and metabolic demands, examination of the influence on the behavioral ecology of fishes has been largely restricted to thermoregulation and the triggering of seasonal migrations (following Reynolds, 1977). Two limited field studies have examined the effect of temperature on flatfish movements. Swimming activity of sole and winter flounder, measured using ultrasonic telemetry and visual observation around baited hooks, respectively, decreased at lower temperatures (Lagardére and Sureau, 1989; He, 2003). The present study is the first to examine the direct effects of water temperature on the behavioral ecology of a flatfish.

While the crepuscular activity peaks occurred in all temperature treatments, our observations demonstrate a thermally induced change in day–night activity patterns (Fig. 5). The largest effect of water temperature on activity patterns of juvenile northern rock sole
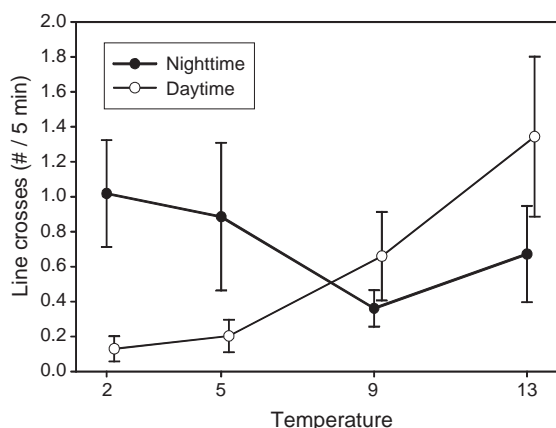
Fig. 5. Temperature-dependent pattern of daytime and nighttime activity in juvenile northern rock sole. Open and filled circles represent the mean frequency of daytime and nighttime line crossings, respectively. Error bars indicate 1 S.E. of mean from 5 replicates at each temperature.

was a reduction in daytime and crepuscular activity at low temperatures. The frequency of line crossings during daylight and the dusk–dawn transitional periods at 2 °C was only 10% and 28%, respectively, of those observed at 13°. Conversely, there was a trend toward higher counts of nighttime line crossings at lower temperatures. There was also a moderate (but statistically significant) effect of water temperature on the mode of activity at night, as the fraction of line crossings made in the water column increased from 80% at 13° to 93% at 2°. At high temperatures, rock sole activity occurred primarily during daylight hours and was largely confined to within a few centimeters of the sediment surface. At low temperatures however, nighttime activity was favored with water column swimming representing a major component of total daily activity.

Seasonal, ontogenetic and temperature induced changes in circadian activity rhythms have been observed in several other species. Whether a single mechanistic explanation holds across species is unclear (Reebs, 2003). In the Temperature Trials presented here, all observations were made from 48 to 72 h after the last feeding to eliminate the short-term effects of feeding described in the Feeding Trials. While, northern rock sole are able to maintain positive growth at 2°, feeding rates are well below those observed at higher temperatures (Hurst and Abookire, in review). As a result, hunger level likely

differed among the temperature treatments due to variation in metabolic processes, potentially influencing our results. While not related directly to hunger per se, a similar change from diurnal to nocturnal activity at low temperatures in Atlantic salmon *Salmo salar* (L.) (Fraser et al., 1993) and European minnows *Phoxinus phoxinus* (L.) (Greenwood and Metcalfe, 1998) is believed to reflect a balancing of energetic requirements with diel variation in vulnerability to predation (Metcalfe and Steele, 2001). A change from diurnal to nocturnal activity observed in tautog *Tautoga onitis* (L.) during temperature decreases was believed to be associated with the autumnal migration away from nearshore habitats (Olla and Studholm, 1978).

Water temperature also had a significant effect on swimming speed during voluntary nighttime swimming. Speeds (in bodylengths per second, BL s^{-1}) measured in Temperature Trials by digitizing rock sole swim paths increased from 0.71 ($\pm$0.03 S.E.) at 2° to 0.94 ($\pm$0.04) at 13°. While there are few measurements of voluntary swimming speeds of flatfishes, maximum speeds have been measured in several species. Modest swimming speed increases with temperature were noted for plaice, flounder *Platichthys flesus* (L.) and American plaice *Hippoglossoides platessoides* (Fabricius) (Priede and Holliday, 1980; Duthie, 1982; Winger et al., 1999) but not for lemon sole *Microstomus kitt* (Walbaum) and dab *L. limanda* (L.) (Duthie, 1982).

4.4. Feeding effects

Feeding had significant short-term effects on the activity levels of northern rock sole, but did not disrupt the general pattern of crepuscular peaks. Previous observations of flatfishes have indicated that feeding resulted in immediate increases in activity followed by prolonged periods of inactivity (Creutzberg et al., 1978; Champalbert and Le Direach-Boursier, 1998). Our results with northern rock sole fed during the day or at dusk produced similar patterns. Following feeding, fish remained motionless for an extended period, resuming activity during the subsequent crepuscular period. Contrary to the observations of Champalbert and Le Direach-Boursier (1998) for juvenile turbot, nighttime feeding in rock sole was not followed by a period of inactivity.

Activity of rock sole increased following the addition of food in the dark and remained elevated for several hours, after which, activity levels fell back to pre-feeding levels for the remainder of the dark period. While we could not discern food particles and iden-tify feeding activity from videotapes, the continued activity of night-fed rock sole suggests a reduced foraging efficiency in the dark, requiring a longer time to reach satiation.

If rock sole use water column swimming activity as a mechanism for locating suitable foraging habitats (Creutzberg et al., 1978), we would expect this be-havior to be particularly sensitive to feeding history. Among fish in the daytime feeding treatment, 68% of nighttime line crosses were made swimming in the water column. Feeding at dusk suppressed all night-time activity, not just water column swimming. Counter to expectations, nighttime feeding did not reduce the incidence of water column swimming. The reduced fraction of line crossings made in the water column following the addition of food at night was due to an increase in the number of benthic line crossings rather than a reduction in water column activity.

5. Conclusion

Northern rock sole exhibited a temporal segrega-tion of activity mode. Fish restricted daytime and crepuscular activity to the benthos, likely reflecting foraging behavior, but made frequent, prolonged excursions into the water column at night. Such nighttime activity has been observed in juveniles and adults of other flatfish species, although the function of this behavior remains poorly understood. As observed in other flatfishes the activity patterns of juvenile northern rock sole were affected by in-ternal (feeding history) and external (temperature) conditions (Hurst et al., 2005). While these factors impacted activity levels at all times of day, they did not alter the dominant crepuscular periodicity of activity. This crepuscular activity peak may represent a mechanism of balancing light-dependent foraging efficiency with predation vulnerability. Additional studies are currently underway examining the rela-tionships between the activity patterns observed in these laboratory experiments, visual acuity and diel patterns of foraging and habitat selection in juvenile northern rock sole.

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